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THE NERVOUS CENTRE OF FLIGHT IN COLEOPTERA.

IS IT possible to know the physiology of an organ, that is to say, its functions, signification, and purpose, from a simple study of its anatomy? Eminent authors have said no to this question. Claude Bernard, the greatest physiologist of the century, especially, has contemned the assistance of anatomy in the understanding of the phenomena of life, and his ideas are generally accepted, having passed as authoritative into the standard works on the subject. To a great extent, this position is the correct one. It is incontestable that the majority of physiological discoveries have been made by physiology. I propose, however, to show that this rule admits of exceptions, and that we can, in certain circumstances, where it is impossible to resort to vivisection, apply the method of comparative anatomy to the solution of very nice problems of nervous physiology.

The philosophical interest of this method will make ample recompense for the dryness of details which the study of the nervous centre of flight in *Coleoptera* presents; for this is the investigation of which we are now about to give a sketch. We announced some time ago our intention to do this, in an article published in Vol. III, No. 1, of *The Monist*, where we sought to sketch the outlines of the normal structure of the ganglion.

It will be well, perhaps, briefly to recall at the outset the general disposition of the wings and the nervous system of *Coleoptera*. We know that these insects possess two pairs of wings, which are inserted in the dorsal face of the thorax. The posterior pair alone

serve for flight. They are composed of a fine, transparent membrane, supported by delicate nervures. The anterior wings, which are called "elytra," are sheaths of greater or less powers of resistance, sometimes speckled with bright colors, covering the wings when at rest and protecting them after the manner of a buckler. When the animal takes to flight the elytra spread, so as to permit the membranous wings to unfold.

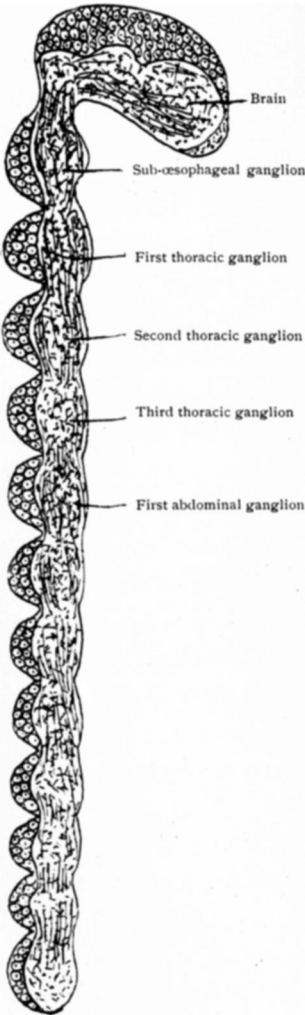


Fig. 1.—Schematic longitudinal section of the nervous system of a larva of a dipteran.

Each of these two organs is joined by a rather large nerve with the nervous system of the insect. This nervous system, which is of a quite complex character, is composed of a brain situated in the head, whence a nervous ring, encompassing the digestive tract, proceeds. This nerve-ring connects the brain with a chain of nerves that extends beneath the digestive tract the entire length of the ventral face of the insect and widens into a series of ganglia. This chain of nerves forms what is called the sub-intestinal nervous system. We may obtain some sort of an idea of this system of organs by casting a glance at Fig. 1, which represents the nervous system of the larva of a dipteran.

The first ganglion of the sub-intestinal chain is called the sub-oesophagean; it innervates the buccal parts and is usually located in the head of the animal. The second, third, and fourth ganglia, in the adult insect, are usually situated in the thorax; they are called the thoracic ganglia. These ganglia send out the nerves to the three pairs of

feet; they are consequently the locomotor ganglia. Next comes the abdominal chain of ganglia, which furnishes nerves to the cells of the abdomen and to the genital regions.

At present, the thoracic ganglia chiefly interest us, as these furnish the nerves of the wings and elytra. These ganglia are three in number. The first is not connected with the apparatus of flight, and, consequently, does not interest us; the second supplies the nerves of the elytra; and the third, the nerves of the wings.

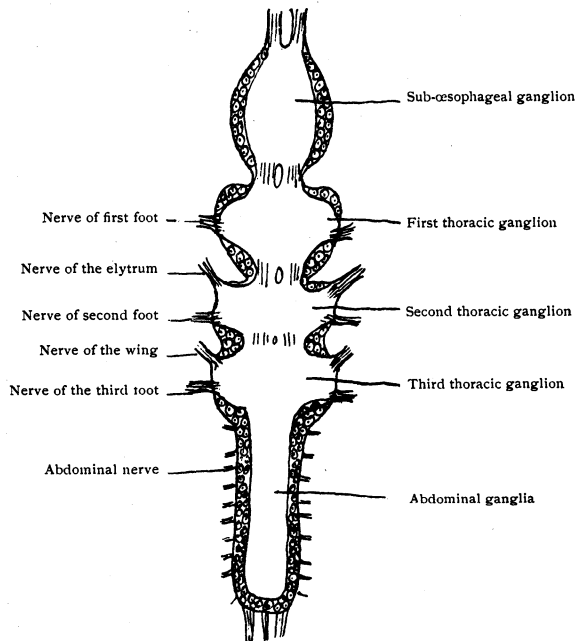


Fig. 2.—Schematic horizontal section of the sub-intestinal nervous system of *Rhizotrogus*.

The appended cut, which represents a horizontal section of the sub-intestinal nervous system of a coleopter (*Rhizotrogus*), shows the series of ganglia which we have just described, with the nerves that proceed from it. It will be noted that the second and third thoracic ganglia give out, respectively, the nerves of the elytra and of the wings.

This is a synopsis of the knowledge which the dissection of an insect with the scalpel furnishes us; to obtain any knowledge of

the internal structure of a ganglion, we are obliged to resort to the method of sections, which consists in cutting up an organ in slices sufficiently thin to allow of their being studied in a transparent form under the microscope. In any *section* of a ganglion, taken in any plane, it will be seen by such an examination that the small mass of nervous substance constituting the ganglion is always composed of the two following parts: a central part, of considerable size, composing three-fourths of the ganglion and made up of fibrillar sub-

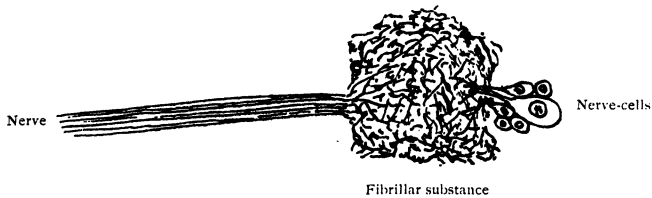


Fig. 3.

stance; and about it a second part, formed of nerve-cells, the number and size of which vary with the place. These cells give out prolongations, which lose themselves in the fibrillar substance. It is a conclusion to which precise researches directly point, that the

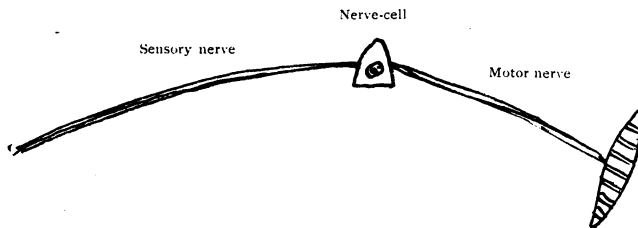


Fig. 4.

nerves which lead to a ganglion do not end directly in the cells, but in the fibrillar substance; and similarly the axial prolongations of the cells do not directly continue into the nerves, but are also lost in the fibrillar substance. This is schematically represented in Fig. 3. It will be at once seen that this histological arrangement greatly differs from the plan of the reflex arc (Fig. 4), which is now everywhere described, but is probably very inexact. According to the plan usually given, the sensory nerve ends directly in the nervous cell, which reflects the excitation to the motor nerve. The

nervous excitation follows a path presenting no solution of continuity. But, as a fact, in insects there is a something interposed between the nerve and the nervous cellule, and this something is the fibrillar substance, which is made up of a skein of fibres so complicated in structure, that it is hopeless to attempt to disentangle it. Consequently, we are in total ignorance as to whether a continuity exists between the nerve and the cell, or whether the excitation is not otherwise propagated between the two points.

Leaving aside this important question of nervous histology which is now occupying the attention of a host of observers, let us follow the alary nerve into the interior of the ganglion and see how it acts towards the organs which the ganglion contains. We shall now be obliged, in the interest of clearness, to say a few words concerning the internal organisation of a thoracic ganglion, but we shall

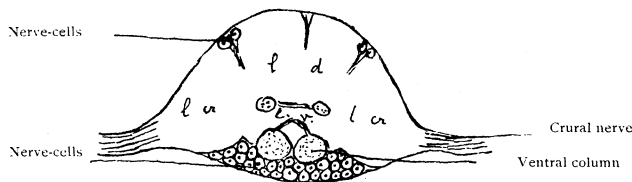


Fig. 5.—Schematic transverse section of a thoracic ganglion of an Insect.

restrict ourselves in this to what is absolutely necessary to an understanding of the plan of the alary nerve, and shall accordingly reproduce, very briefly, the substance of our preceding article. A thoracic ganglion may be regarded as made up of the following three distinct parts (in this description we shall only occupy ourselves with the fibrillar substance): a ventral lobe, a dorsal lobe, and, laterally, of two crural lobes. The crural lobes are connected with the nerves of the feet; these we shall not discuss. A difference of the dorsal and ventral lobes is seen at once by a glance at their fibrillar substances. This substance is quite tenuous in the dorsal lobe; while in the ventral lobe it is very dense, clearly outlining a special organ to which we have given the name of *ventral column*. In Fig. 5, which is a transverse section, we see, at the sides, the two crural lobes (marked *l. cr.*), in which the nerves of the feet end; higher up the dorsal lobe; and, beneath, the ventral lobe, which displays a cir-

cular section of the two ventral columns. And in the longitudinal section (Fig. 6), that is to say, in a section parallel to the flanks of the animal, the ventral column appears in its characteristic form of a column elongated along the ventral region of the ganglion; and above it in the dorsal lobe will be seen the connective filaments which traverse the ganglion longitudinally, and extend throughout the whole subintestinal nervous chain. Finally, a horizontal sec-

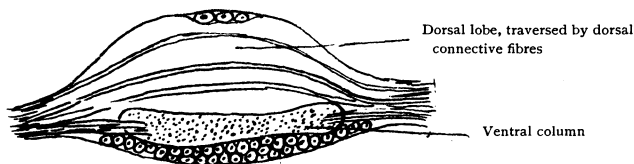


Fig. 6.—Schematic longitudinal section of a thoracic ganglion of an Insect.

tion, made parallel to the ventral face of the insect, shows that the ventral column is double and symmetrical. There exist, in fact, two ventral columns, situated one on each side of the median line;

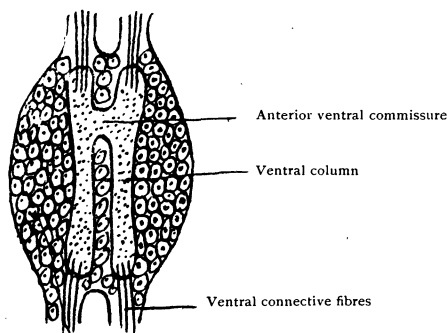


Fig. 7.—Schematic horizontal section of a thoracic ganglion of an Insect, showing the two ventral columns.

and this duality is evidently in some way connected with the primitive duality of the ganglion, which is developed in two distinct parts (Fig. 7).

The path of the alary nerve into the interior of the ganglion is sufficiently defined by these details. This nerve, considered for example in the cockchafer, penetrates the lateral regions of the upper face of the ganglion; then, after having passed the conjunctive envelope of the ganglion, it emits its extremely slender first root

which enters the upper parts of the dorsal lobe where it is accompanied throughout its entire course by a great number of tracheæ, amid which it is scarcely discernible; this is the *upper dorsal root* of the alary nerve. Then the trunk of the nerve continues its oblique course and descends; it traverses the bed of nerve-cells which surrounds in this region the fibrillar substance, and penetrates that substance. At this point it is subdivided into two roots, both much larger than that which we above described. The first of these roots

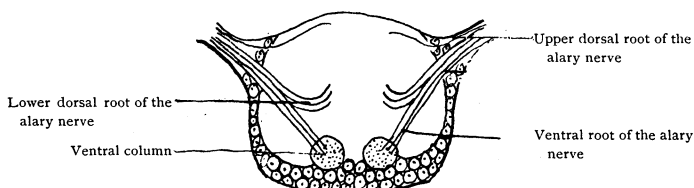


Fig. 8.—Schematic transverse section of a thoracic ganglion of a coleopter, showing the three roots of the alary nerve.

describes the small arc of a circle curved concavely upwards and rises again towards the dorsal lobe of the ganglion. This is the *lower dorsal root* of the alary nerve. The other makes directly towards the ventral column, which is its ultimate destination. This

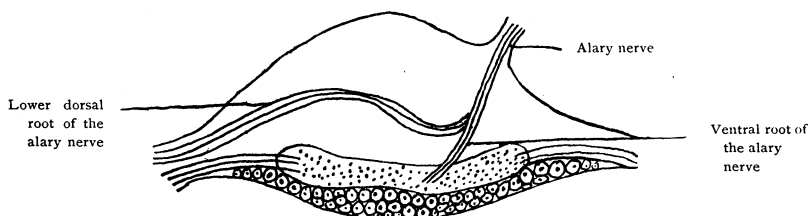


Fig. 9.—Schematic longitudinal section of a thoracic ganglion of a coleopter showing two roots of the alary nerve.

is the *ventral root* of the alary nerve. The disposition of these three roots is distinctly seen in a suitably taken transverse section like that of Fig. 8.

In some types of *Coleoptera*, for example, in the horn-beetle, it has been found that the ventral root is double. To determine the course of the lower dorsal root, which we have good reasons—to be mentioned later—for regarding as the characteristic root of the alary nerve, we must follow its path in an appropriate longitudinal section, i. e., in one which is slightly oblique (Fig. 9). In such a sec-

tion we find that this root crosses the ganglion from the front to the rear and enters the succeeding ganglion, which is the third thoracic ganglion. Here, all knowledge which microscopic anatomy furnishes us concerning the roots of the alary nerve ceases. Can we go any further, can we learn anything concerning the function of these roots ?

We already possess some interesting facts concerning the physiology of the thoracic ganglia of insects. These facts are due to the fine and precise researches of Faivre, a naturalist as eminent as he is modest, who has, perhaps, not yet acquired the full reputation which is his due. Faivre has long studied, with a sort of predilection, the genus *Dytiscus*—the coleopter of marshes and swamps, the water-beetle, which owing to the facility with which it may be procured at all seasons, and also owing to its large size, seems almost predestined for vivisection, and may be almost regarded as the frog of the invertebrates. Faivre has minutely studied the properties of all the nervous ganglia, of the connective filaments, of the nerves, and even of the stomato-gastric system of this animal. He is ignorant of the internal structure of the parts on which he experimented. The method of sections was not practised at that period. He simply connected the effect of the irritations, punctures, and experimental lesions which he made with the exact point that had been injured. He has traced, thus, a *topographical physiology*, the precision of which in my judgment is admirable, as every time that I have repeated his experiments I have arrived at exactly the same results. We shall not speak here of his researches on the stomato-gastric system, nor of those on the brain, in which he defined the boundaries of the motor centre of the antennæ at a time when men were still ignorant of the existence of the deuto-cerebrum. We shall simply restrict ourselves to a recapitulation of the results obtained by him in his experiments on the thoracic ganglia.

Guided doubtless by the idea of an analogy between the functions of the sub-intestinal nerve-ganglia of insects and the functions of the spinal marrow of vertebrates, Faivre sought to discover whether the outermost peripheral face of the ganglion of an insect was not endowed with especially sensitive properties, and the face

farthest inwards with especially motory properties. We need scarcely recall to the reader's attention the well-known fact that in insects, viewed in the natural position of locomotion, the nervous system of the thorax and the abdomen is sub-intestinal, while in vertebrates the nervous system is situated wholly above the digestive tract, and that, consequently, the face of this system which is nearest the periphery of the body is ventral in insects and dorsal in vertebrates; in other words, the development of the nervous system which is effected in parallel lines in the two types of animals at the expense of the ectodermal layer, takes place for the sub-intestinal ganglia of insects in the ectoderm of the ventral regions, and for the vertebrates in the ectoderm of the dorsal region. The result of this disposition is, that the ventral face of the ganglion of an insect is the homologue of the dorsal face of the spinal marrow; and Faivre has effectively shown that these two faces are possessed of the same sensitive properties.

The experiments of Faivre bear especially on the movements of the feet, which are quite easy to observe, and which are much more varied than the movements of the wings or the elytra. The experimenter first established that the sensibility of a foot and its powers of motion can be destroyed separately. Lesions or simple irritations may be made, so localised that the same foot when excited directly will remain at rest, but when the irritation is made elsewhere, on another foot, or on an antenna, or on the pegidium, will move with vivacity. The interpretation of this case is that the foot, not responding to direct excitations, has lost its sensibility, but conserved its powers of motion. Conversely, the lesions may be so localised that a foot will remain absolutely motionless and inert in all cases, as well during direct excitations of itself or other feet as during spontaneous movements of the animal, yet the localisation be such that by irritating this foot a motor effect is produced in other parts of the body. In this case sensibility is preserved but the power of motion lost.

It is possible, thus, notwithstanding the opposite opinion of a number of modern physiologists, to destroy separately each of the two functions sensibility and motion, which are not so indissolubly connected as is generally supposed.

To produce these two inverse effects Faivre found, after many attempts, a precise place for the lesion. The best means appeared to him to be a slight pressure with a flat lancet on one of the faces of the ganglion. The compression of the dorsal face, or a very superficial puncture of that face, or the insertion of the blade under the perineurium produces simple motor paralysis without anæsthesia ; the compression of the ventral face produces anæsthesia without loss of the power of motion. The last symptom, it seems, is more difficult to provoke, and it is necessary to take great pains in not overdoing the compression if we wish to obtain an anæsthesia wholly free from movement. Let us add that these phenomena of paralysis are frequently transitory and disappear in a few hours ; but their duration is sufficient to admit of exact observations, which gain the conviction of the experimenter. We have continued the experiments of Faivre by a new method, which we shall not enter into here, and have found results which are absolutely exact.

We now propose to show that we can arrive at the same conclusion by comparative anatomy. To discover whether this organ is motory, and that sensory, we may dispense with physiological experiments and replace the scalpel by the microscope. Without making a lesion, which destroys the natural disposition of the organs, we can, by simply describing the microscopic section, read in that section the physiological significance of certain structures. This method of comparative anatomy goes much further, it seems to me, than that of Faivre. In the first place, it is more precise, as it replaces an experiment, that is to say, a transitory phenomenon, of which soon afterwards only the memory is left, by the observation of a permanent preparation. Further, the vivisections of Faivre referred only to a part or region and not to an organ. To establish that the ventral face of a ganglion is sensory is only an approximate result. What internal organs of a ganglion does this face comprise? Where does it stop? And as many more questions, to which no answer can be given by the scalpel. But comparative anatomy, as we shall see, is not content with pointing out the sensory region ; it also determines the organ and the nerve.

Let us see, now, how this anatomical demonstration can be ef-

fect. We have directed our attention to certain coleopters which present the interesting characteristic of possessing wings and of not making use of these for flight or for any other movement. An appellation is wanting for these coleopters, and we have accordingly supplied them with one: Aptesids, from *a*, privative, and *ptésis*, flight, to point out their chief deficiency, which is not the lack of an organ, but of a function. Our examination is restricted to three of these coleopters of quite different families, namely: *Blaps mortisaga*, *Timarcha tenebricosa*, and *Carabus auratus*.

In these three species the membranous wings are wanting. The elytra exist, but are immobile and generally soldered together at the median line. These organs conserve their office of affording protection for the abdomen. There is a curious instance of disassociation here between sensibility and motion; the elytrum has remained sensory, but has lost the power of motion.

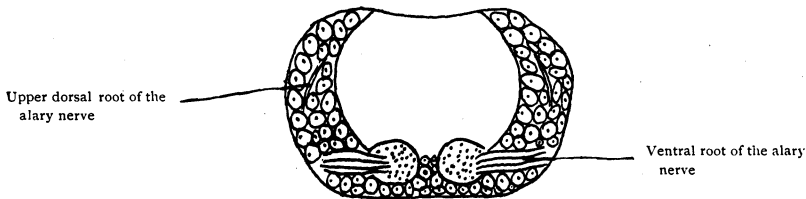


Fig. 10.—Schematic transverse section of the second thoracic ganglion of *Timarcha tenebricosa*.

It is natural, then, that we should seek the extent to which this physiological modification has affected the internal structures of the ganglion. The idea of such an investigation would never occur to us, if we did not know that insects of the same order are comparable one with another, and if our studies had not already informed us that a thoracic ganglion, for example, has much the same organisation in all coleopters. We can, then, legitimately suppose that the roots of the alary nerve present the same disposition in a coleopter that flies and in a coleopter that does not, and that the differences which may exist between the two cases should be attributed to the physiological modification referred to.

Let us now cast a glance at a transverse section, seen in Fig. 10, of the second thoracic ganglion of *Timarcha*. We see that the

roots of the alary nerve have suffered considerable reduction. The upper dorsal root subsists. The ventral root also subsists, with important diminutions, which we already know about. The suppression continues to the intermedial root and to the lower dorsal root, whose strange course we have described above.

We have not traced this root on the drawing, because we have not been able to find it in our preparations. Has it wholly disappeared? We shall not answer this question in the affirmative. It is sufficient to cast a glance at the tangled mass of fibres of one of these preparations,—which our drawings always simplify and schematise,—to understand how dangerous it would be to deny the existence of fibres which could escape the most practised eye. Still, a negative result should, with reservations, always be admissible. The only conclusion to be insisted upon is—and this conclusion is quite sufficient to serve as the basis of our physiological deductions—that if there exist in the ganglion of an aptesic coleopter fibres representing the lower dorsal root of the alary nerve, these fibres must be greatly reduced in number and in importance, for while a lower dorsal root is discovered with great facility in a ganglion which possesses the power of flight, here these fibres are not at all distinctly discernible. If, at some future day, by means of more perfect technical methods, we succeed in clearly distinguishing these fibres, it will yet always be exact to say that the loss of the power of flight in *Timarcha*, *Blaps*, and *Carabus* is especially indicated in the lower dorsal root, and that consequently this root should be considered as motory in character.

This is the main conclusion which we are now in possession of, and one which will serve us as a point of departure for a whole series of deductions. But, before accepting it, it will be best to seek the criticisms which can be advanced in connexion with it.

If the lower dorsal root is motory, the ventral root is sensory; these two conclusions are inseparably connected. We may ask, in this connexion, what can be the nature of the slender root which goes to the upper dorsal region of the ganglion, and which exists in *Timarcha*. It is too far removed from the ventral root to be endowed with sensory properties. Should it be considered motory?

This supposition appears to be contradicted by the fact that the elytrium is immobile and has no need of a motor nerve.

This slight difficulty of interpretation appears to us to find its solution in a remark which must be made concerning the constitution of the alary nerve. This nerve is not wholly composed of fibres which go to the wing; branches proceed from the alary nerve, which distribute themselves in the walls of the body. The alary nerve is thus a nerve at once alary and parietal; and it is probable, therefore, that the upper dorsal root belongs to the parietal fibres.

It now remains to be known how the alary nerve is represented in the third thoracic ganglion of the aptesic coleopter. The third thoracic ganglion supplies the nerves of the membranous wings. These latter, we have said, are wanting in *Timarcha*, as also in two other aptesic coleopters. Fig. 11 represents a transverse section of

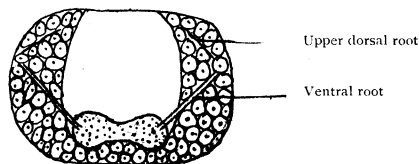


Fig. 11.—Schematic transverse section of the third thoracic ganglion of *Timarcha tenebricosa*.

the third thoracic ganglion of *Timarcha*. It will be seen that the alary nerve is represented here by two roots, exactly as in the second ganglion; only,—and the difference is one of great importance,—that while in the second thoracic ganglion the ventral root of the alary nerve is very voluminous, here, in the third ganglion, it is much attenuated.

Now, keeping this feature in mind, it appears that we may compare this nerve in its attenuated form to one of the parietal nerves which we found in the series of the abdominal ganglia. The abdominal nerves are apparently composed of two slender roots of which one extends into the upper parts of the dorsal lobe, while the other terminates in the dorsal column. The resemblance is indeed so perfect that Fig. 11 might represent indifferently a section of the anterior region of the third thoracic ganglion and a section of the abdominal ganglion.

This permits us to make, in passing, an instructive comparison between an abdominal (or parietal) nerve and the alary nerve. These two types of nerves have a common root, the upper dorsal root. They also have a quite analogous second root, the ventral root, which is thin in an abdominal nerve, but quite voluminous in an alary nerve. What characterises the latter, is the presence of the lower dorsal root, which is not represented at all in an abdominal nerve. We may say—neglecting slight differences—that the alary nerve is an abdominal or parietal nerve, to which a lower dorsal root is added.

This resemblance seems to us confirmed in a very distinct manner by an observation which we have made on the thoracic ganglia of the larvæ of *Coleoptera*. We were curious to know in what form an alary nerve appeared in the larvæ, which, as is well known, possess no wings. Fig. 11 could also represent, just as faithfully, a section of a larval thoracic ganglion taken at the level of the anterior region; that is to say, the alary nerve is represented in the larvæ by a parietal nerve. Again, embryogeny supplies a further confirmation of these deductions, by showing us that the wing is not, like the leg, a real appendage, but is produced from the wall of the z-onite, which at the points where this development does not take place is innervated by a parietal nerve. But let us leave these incidental considerations and return to our main subject.

We may consider it for the present an established fact that the alary nerve has a sensory root, namely, the ventral root, and a motor root, namely, the lower dorsal root. This conclusion, we see, is in perfect accord with the experiments of Faivre, who has established that the ventral face of the ganglion is endowed with sensitive properties, and the opposite face with motor properties. Our conclusion goes much further, for instead of referring us to a province that is undefined, it points out to us with absolute precision a tangible bundle of nerve-fibres.

Knowing the nature of these fibres, we can, by examining the lobes in which they terminate, learn by inference the physiological properties of the lobes. It is thus that the ventral column receiving the sensory fibres must be considered as an organ of sensation, while

the dorsal lobe which receives the motor fibres is certainly a centre of motion.

This is not all. Observation shows that the fibres that traverse the ventral column from the front to the rear do not fuse in the connective filaments with the fibres that traverse the dorsal lobe of the ganglion. The inference from this is that the dorsal region of the connective filaments is motory, and the ventral region sensory.

Continuing our deductions, if we examine the brain of the insect, we shall observe that it includes a region, the fibrillar substance of which has the same loose texture as the dorsal lobe of a sub-intestinal ganglion, and also a second region where the fibrillar substance is as dense as in the ventral column. Owing to the cephalic curvature, these regions present a substantially different disposition, and the ventral region of the sub-intestinal ganglion is represented in the brain by the anterior region; similarly, the dorsal region of the sub-intestinal ganglion becomes the posterior region in the case of the brain. These homologues, vague as they at first may appear, possess at least the interest of showing that in the most complex ganglia of the nervous system of insects, in those ganglia that are incontestably the seat of high psychical functions, we find the same divisions of sensory and motory centres.

We shall close by remarking that there exists in the brain of insects a very large body on which anatomists have bestowed the name of pedunculate body, but whose functions, despite some curious observations, have hitherto remained an enigma. It is regarded as incontestable that the pedunculate body is an organ of psychical functions, as it only exists in the first brain and is not in connection with the nerves of special senses; and also because, as the beautiful researches of M. Forel on ants have shown, the development of this body seems to be greater in proportion as the insect is more intelligent. Our studies of the alary nerve make an important addition to the ideas hitherto held on this subject. In view of the fact that the pedunculate body belongs almost entirely to that region of the brain which we may consider sensory and which is the homologue of the ventral column, we believe it can be maintained that the pedunculate body is a sensory organ. ALFRED BINET.